Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

REVERSAL OF CLEAVAGE IN ANCYLUS.

SAMUEL J. HOLMES.

THE fact discovered by Crampton that in Physa, a genus of sinistral gasteropods, the direction of the early divisions of the ovum is just the reverse of the corresponding cleavages in the dextral forms suggests, as Crampton pointed out, that there may be some correlation between the reversed cleavage of the ovum and the reversed asymmetry of the adult. The reversed asymmetry of Physa is shown, not merely by the sinistral coil of the shell, but also by the arrangement of the organs of the body. In most gasteropods the anal and genital orifices open on the right side of the body, but in Physa their position is on the left side; and the lung cavity, normally on the right side in the pulmonates, opens on the left in Physa. In fact, the asymmetry of the sinistral form seems in all respects just the reverse of that of the dextral forms. In Planorbis, a genus in which there is a reversal of the position of the organs of the body, although the shell is often coiled in one plane or even dextral (pseudo-dextral), the cleavage of the ovum is of the same reversed type as in Physa. This reversal is shown as early as the second cleavage of the egg which leads to the four-cell stage. Even before there is any elongation of the dividing cell, or any external indication of cleavage whatever, the direction of the approaching division is shown by the inclination of the nuclear spindles. This early indication of the direction of division is shown in the two-cell stage in Crepidula, Limax, Lymnea, and Amphitrite, but in all these cases in which the cleavage is of the dexiotropic or normal type the inclination of the spindles is the reverse of that in Physa and Planorbis. As a consequence of this oblique division, we have probably in all forms with typical spiral cleavage a four-cell stage in which two of the cells lie at a somewhat lower level than the other two and meet in a cross furrow at the vegetal pole. The lower part of the first cleavage plane, when viewed from the animal pole, bends at this cross furrow in the dextral forms, first to the right and then to the left; in the sinistral forms the bend is first to the left and then to the right. When we know, therefore, between which cells the first cleavage plane runs, the four-cell stage, produced by reversed cleavage, can be distinguished at a glance from a four-cell stage of the normal type. The one is the mirrored image of the other.

It is a remarkable fact that, not only in all dextrally coiled gasteropods whose cleavage has been carefully studied, but in many groups characterized by a typical bilateral symmetry, such as the lamellibranchs, Amphineura, annelids, and polyclades, the cleavage is uniformly dexiotropic. The two sinistral gasteropods, Physa and Planorbis, form, I believe, the only instances in which, up to the present time, a reversed spiral cleavage is known to occur.

It was with the desire of obtaining more data bearing upon this subject that I was led to study the cleavage of Ancylus, the common fresh-water limpet. In this genus the coil of the shell is almost entirely lost, and in some forms the shell appears to possess an almost perfect bilateral symmetry; but in many species of the genus the animal is truly sinistral, as the heart, lung, and anal and genital openings lie on the left side of the body. The genus contains both dextral and sinistral forms and has been divided into several subgenera, Ancylus proper containing the sinistral species, while the subgenus Acroloxus comprises only those that are dextral. The species studied, *Ancylus rivularis* Say, belongs to the sinistral group and is found in considerable abundance in a small lake near Ann Arbor, Mich. Specimens taken September 12, and kept in glass dishes in the laboratory, deposited eggs in the sides of the vessel, but not in any great number. The eggs are laid in minute, transparent, colorless capsules, each capsule, unlike that of the European species *A. fluviatilis*, containing but a single egg. The capsule is covered by a membrane and contains a semi-fluid, gelatinous substance in which the egg floats similar to that which surrounds the egg of Physa or Lymnea. It is a difficult matter, on account of its small size and the toughness of the membrane, to get the egg out of the capsule without injury, and the chance of losing it in the process of fixation, staining, etc., before it is safely mounted, is very considerable, so that no attempt was made to carry the cleavage very far. At the first cleavage the egg divides into two equal cells, which round off in the usual manner and then become more closely approximated shortly before the division into four cells. The eight-cell stage is formed by the unequal division of the four cells, each cell giving off a smaller clear cell at the animal pole. This cleavage is an oblique one, the daughter cells lying in the angles between the larger cells. The smaller cells do not lie exactly midway between the larger ones, but more nearly over the cells from which they arose. The next cleavage takes place in the four larger cells or macromeres, and, as indicated in Fig. 2, the direction of cleavage is shown to be in a right-handed spiral by the inclination of the spindles — just the reverse of the corresponding cleavage in the unreversed type. The cleavage of the egg was not followed beyond this point, but it is very probable that the subsequent divisions would show the same reversal. In Physa, according to Crampton, every division as far as the twenty-eight-cell stage is the reverse of the corresponding division in the closely allied genus Lymnea, and in Planorbis, in which I have followed the cleavage in detail to beyond the 150-cell stage, the reversed type of cleavage holds, except in one or two divisions, as far as the cleavage is of a determinate spiral character.

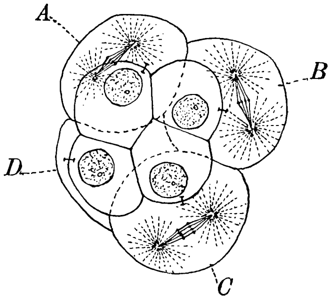

FIG 1. — Eight-cell stage seen from the animal pole.

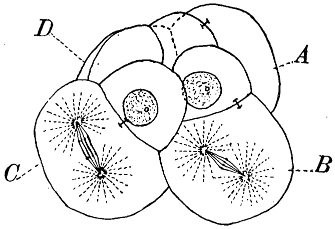

FIG. 2. — The same egg seen obliquely, showing the dexiotropic inclination of the spindles in the dividing macromeres. The cell *C* has begun to elongate.

It is one of the striking features of the cleavage of many mollusks and annelids that certain cells of the upper side of the egg become so arranged as to produce the appearance of a cross, the center of which lies at the apical pole. It was found by Conklin that the arms of the cross in Crepidula are not exactly meridional in position, but have a slight dexiotropic twist. This twist Conklin considered as an expression of the dexiotropic cleavage of the egg, and the fact that the same inclination of the arms of the cross has been found by Heath in Ischnochiton, a form with the same type of cleavage, tends to confirm this view. In Planorbis, on the other hand, the inclination of the arms of the cross is very plainly læotropic, and this twist may be seen as late as the end of the period of gastrulation. A careful comparison of the genesis of the arms of the cross in these forms would convince any one, I believe, that the different directions of the inclination of the arms is correlated with the different types of cleavage. As a result, therefore, of reversed cleavage a considerable portion of the embryo becomes subjected to a torsion in a direction different from that which occurs in the normal forms. It does not seem possible in Planorbis to connect directly this torsion of the cross with the sinistral organization of the animal, for this structure disappears before the asymmetry of the embryo is manifest. However, the fact that reversal of cleavage shows its effects as late as the gastrula stage lends considerable support to the view that it may stand in some causal relation to the reversed asymmetry of the adult.

In Crepidula, Conklin has succeeded in tracing the beginning of the asymmetry of the embryo to the division of one of the cells of the entoderm. The time and direction of this cleavage were found to give the initial twist to the rudiment of the intestine. "If," says Conklin, "the initial asymmetry is caused in Physa, as in Crepidula, by the asymmetry of the cells *5C* and *5D*, then it is easy to see how this reversal of cleavage stands in a causal relation to the reversed asymmetry of the adult." In Planorbis the corresponding divisions result in the formation of very small cells instead of large, yolk-laden ones, as in Crepidula, and do not seem to exercise any influence in determining the asymmetry of the embryo. The cells of the entoderm become very numerous (over thirty) and of small size before gastrulation occurs, and it seems impossible to connect the asymmetry of the adult with any of their divisions. The læotropic inclination of the arms of the cross in Planorbis is probably the expression of a torsion that affects, to a certain extent, a large part of the segmented ovum, and the reversed asymmetry of the adult may depend upon this general twist, rather than the reversed division of any of the cells of the entoderm. It is not improbable that the asymmetry of the animal may first manifest itself, as the results of various investigations indicate, in different parts of the embryo in different forms.

The reversal of cleavage in Ancylus has, I believe, a special significance from the fact that the left-handedness occurring in this genus has, in all probability, arisen independently of that of Physa and Planorbis. It may, indeed, be doubted whether the reversed asymmetry of the latter genera is due to their descent from a common sinistral ancestor; but, however this may be, it is scarcely possible that Physa, Planorbis, and the sinistral species of Ancylus all belong to one group which branched off from the dextral species of Ancylus and the other pulmonates. As is well known, we have sinistral individuals occurring as occasional variations among dextral forms, and in the genus Fulgur and in several genera of the terrestrial pulmonates there are well-established dextral and sinistral species. Analogous reversals of asymmetry occur in other groups of animals, such as the flounders, certain nematodes, and many crustaceans, and there appears to be no great improbability, *a priori*, in supposing an independent origin of left-handedness in Ancylus; besides, any other supposition would involve us in improbable phyletic derivations. The chance that the association of reversed cleavage with reversed asymmetry in the gasteropods is a mere coincidence is very much lessened by the circumstance that the same association obtains where the reversed asymmetry has been independently acquired. It would be a matter of interest to ascertain if the cleavage of the dextral species of Ancylus were of the normal type, and if the right-handed and left-handed species of Fulgur and the terrestrial pulmonates, Pupa, Bulimnus, and

Clausilia, have respectively a normal and reversed cleavage. So far as the facts are known at present, they seem to justify the view that the reversed asymmetry of the sinistral gasteropods owes its origin to a reversal of cleavage of the egg.

UNIVERSITY OF MICHIGAN,
October 13, 1899.